PSYCHE

VOL. 54 JUNE, 1947 No. 2

EARLY INSECT LIFE*

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Most entomologists, whether concerned with insect control or taxonomy, are convinced that we have enough living insects to contend with, without bothering about those of prehistoric times. Paradoxical as it may be, however, man apparently owes his very existence to the early insects. Some three hundred million years ago, as the first Amphibia abandoned the aquatic environment of their ancestors and explored the possibilities of terrestrial life, they were obliged to find a new source of food. By that time, the insects had already become established on land and, being especially abundant near water, were readily available to them. The amphibians were thus able to survive in their new environment and eventually their descendants gave rise to reptiles, birds and mammals. Many geologic periods later—only a few million years ago, in fact—man evolved within the mammalian complex. Cannot the insects claim, therefore, that if it were not for their early ancestors, the vertebrates might have failed to gain a foot-hold on land and man might not have come into existence?

Let us consider the nature and extent of the early insect life to which we presumably owe so much. "Early" is of course a relative term, and to define my present use of it, I must refer to the conventional geologic timetable. Figure 1 lists the eras and periods of that part of geologic time with which paleontology is chiefly concerned. Of the three eras, the Paleozoic is the earliest and longest,

* Annual Public Address of the Entomological Society of America, Richmond, Virginia, December 9, 1946. Published with the aid of a grant from the Museum of Comparative Zoölogy at Harvard College.

beginning about 550 million years ago and extending up to some 190 million years ago. For convenience, it is divided into six periods of unequal duration, their limits being arbitrarily set with reference to extensive geologic events. In this account of early insect life, I am referring only to the insects of the Paleozoic era—from the first appearance of the group through the Permian Period.

The question of the oldest geologic occurrence of any group of organisms is always a controversial one, for much depends on interpretation of fragmentary material

TABLE OF GEOLOGIC PERIODS

ERA	PERIOD	APPROXIMATE TIME (IN MILLIONS OF YEARS)	
		DURATION OF PERIOD	SINCE BEGINNING OF PERIOD
CENOZOIC (AGE OF MAMMALS AND MAN)	QUATERNARY	1	1
	TERTIARY	69	70
MESOZOIC (AGE OF REPTILES)	CRETACEOUS	50	120
	JURASSIC	35	155
	TRIASSIC	35	190
PALEOZOIC (AGE OF INVERTEBRATES AND PRIMITIVE VERTEBRATES)	PERMIAN	25	215
	CARBONIFEROUS UPPER	35	250
	CARBONIFEROUS LOWER	50	300
	DEVONIAN	50	350
	SILURIAN	40	390
	ORDOVICIAN	90	480
	CAMBRIAN	70	550

Figure 1. Table of Geologic Periods. (Adapted from Romer's *Vertebrate Paleontology,* University of Chicago Press.)

and the definition of the group. Handlirsch showed in 1906 that the fossils described as insects from strata *older* than those of the Upper Carboniferous Period were not insects at all; and he concluded that the earliest record of the class was in the lower part of that period. During the past forty years discovery of three older insects has been announced. Two of these, identified as Collembola, have been described from Devonian rocks, the Rhynie Chert, of Scotland.[1] Without going into details, we can

[1] R. J. Tillyard, Trans. Ent. Soc. London, 1928: 65–71; H. Womersley, Victorian Naturalist, 1934, vol. 51: 159–165; D. J. Scourfield, Proc. Linn. Soc. London, 152 sess., 1939–40: 113–131.

state that these fossils are very fragmentary, the largest specimen being only about a millimeter long. Many parts of the head and thorax have been found, but since only the first three abdominal segments are known, there is no evidence that the collembolan ''spring'' was present, or that the abdomen consisted of but six segments, as in living Collembola. Consequently, although such eminent authorities as G. H. Carpenter and H. Womersley have accepted the specimens as Collembola, I believe that doubt about their relationship will exist until additional fossils have been found showing those two characteristic features of the Collembola. As a matter of fact, as Imms and others have pointed out, the Collembola are not true insects—that is, although hexapodous arthropods, they arose independently from pre-insectan types. The possible occurrence of Collembola in Devonian rocks, therefore, has no direct bearing on the earliest record of true insects.

The other discovery of an insect in rocks older than the Upper Carboniferous was announced by the French paleontologist, Dr. Pierre Pruvost, in 1919. The specimen concerned was found in Lower Carboniferous strata of Nova Scotia (Horton's Bluff), and identified by Pruvost as a member of the extinct Order Palæodictyoptera.[2] However, examination of this fossil, which is now in the Peabody Museum at Yale University, convinces me that it is in reality part of a plant stem. A similar conviction was expressed by Dr. David White,[3] then paleobotanist of the United States Geological Survey, who studied the specimen shortly after it was found, although he did not publish his conclusion.

According to our present knowledge, therefore, the earliest unquestionable insects occur in Upper Carboniferous strata. This first occurrence is not extensive, but it does indicate the approximate time of origin of the insects. Let us return for a moment to the geologic timetable, and examine in more detail the Upper Carboniferous Period (Figure 2). This represents an interval of

[2] La Faune continentale du terrain Houiller du Nord de la France, p. 283.
[3] In a letter dated May 11, 1914, and on file in the Peabody Museum.

PERIOD	STAGES		INSECT ORDERS
PERMIAN	UPPER		Coleoptera
PERMIAN	MIDDLE		Thysanoptera, Perlaria
PERMIAN	LOWER		*Protoperlaria, Protelytroptera,* Ephemerida, Odonata, Corrodentia, Hemiptera, Mecoptera, Neuroptera
UPPER CARBONIFEROUS	STEPHANIAN		*Protohemiptera*
UPPER CARBONIFEROUS	WESTPHALIAN	C & D	*Megasecoptera, Caloneurodea*
UPPER CARBONIFEROUS	WESTPHALIAN	A & B	*Palaeodictyoptera,* Blattaria
UPPER CARBONIFEROUS	UPPER NAMURIAN		*Protodonata, Protorthoptera*

Figure 2. The First Occurrence of Insect Orders in the Permian and Carboniferous Periods. Names of exinct orders are italicized.

about thirty-five million years, and on the basis of its flora and fauna, is divided into three main stages, the Upper Namurian, Westphalian, and Stephanian. The record of insects is very scanty in the oldest of these; not until the late Westphalian and Stephanian rocks are insect remains sufficiently abundant and preserved to give us a concept of the fauna. Nevertheless, three species are known from the Upper Namurian, at the very base of the Upper Carboniferous, and they constitute the earliest record of the insects. One of these (*Erasipteron larischi* Pruvost), from Czechoslovakia, consists of part of a wing, which, though incomplete, clearly belongs to a member of the extinct Order Protodonata, related to the Odonata. Another fossil (*Stygne roemeri* Handl.), from Germany, is a nearly complete wing with orthopteroid features that place it in another extinct order, the Protorthoptera. The third specimen (*Metropator pusillus* Handl.), from Pennsylvania, is a very fragmentary wing which might have belonged to any one of several orders. Now this is truly a meagre record, but it does reveal two facts: *first,* insects with fully developed wings existed in the earliest part of the Upper Carboniferous Period, about 250 million years ago; and *second,* at least two orders, widely separated phylogenetically, occurred at that time. We can infer from this record that insects must have arisen at least as far back as the Lower Carboniferous in order for such diversity to be attained by the beginning of the Upper Carboniferous. This inference becomes even more obvious, when we bear in mind that morphological studies have shown that the most generalized or primitive insects were wingless, like the Thysanura. Apterous species must have existed, therefore, even before the winged ones.

So much for the first record of the insects. Let us now briefly consider the development of the class during the rest of the Paleozoic era. Referring again to the Upper Carboniferous table (Figure 2) we find that as we go up through the several stages, additional orders appear, and there is an increase in the total number of orders. From the lower half of the Westphalian stage (A and B) there are forty species known, representing the two orders previously mentioned (Protodonata and Protorthoptera), as well as the extinct order Palæodictyoptera and the existing order Blattaria or cockroaches. In the upper half of the Westphalian stage (C and D), about 15 million years after the first record of the insects, we come to the level of the Mazon Creek nodules in Illinois, second only to the Commentry shales in France as a source of Carboniferous insects. From this part of the Westphalian more than four hundred insects are known, representing the four orders already mentioned and in addition two other extinct ones, the Megasecoptera and Caloneurodea. From the Stephanian stage, which includes the Commentry deposit, about fifteen hundred species have been described, belonging to the orders previously mentioned as well as still another exinct one, the Protohemiptera. Thus, we see that by the end of the Upper Carboniferous seven orders of insects had come into existence, of which one, the Blattaria, survived for some two hundred forty million years to the present time.[4]

Let us now continue into the Permian Period (Figure 2), which represents an interval of about twenty-five million years. In the lower or oldest strata of the period eight orders have been found in addition to the seven which have persisted from the Carboniferous. Two of these, the Protoperlaria and Protelytroptera, are extinct, but the others are living orders. These are the Ephemerida, Odonata, Corrodentia, Hemiptera, Mecoptera, and Neuroptera. This fauna was an extremely interesting one, combining as it did eight extinct and seven existing orders. The Lower Permian was the last time, so far as our records now show, that the extinct orders outnumbered the existing ones. In Middle Permian rocks, Thysanoptera and Perlaria have been found; and in upper Permian strata the Coleoptera appear. These make a total of eighteen living and extinct orders of insects which came into existence before the end of the Paleozoic era, about two hundred million years ago; and of these ten are still living.

4 I have not included in this account several extinct orders which are based upon very fragmentary specimens.

This brief survey gives an idea of the extent of the early insect life. The fauna was obviously a complex one—probably more so than we fully realize, for our present roster of the orders existing at the time is surely far from complete. Nevertheless, the variety of insect types probably fell far short of that which exists now, their biological environment being relatively simple. The plants of the time were largely seed-ferns and other gymnosperms; angiosperms were entirely absent, and, incidentally, did not arise for many millions of years later. It is difficult for us, living at a time when angiosperms dominate the plant world, to imagine a time of their complete absence; and equally difficult to imagine an extensive insect fauna without them. Also, there was a complete absence of birds and of mammals. Insects were then the only flying creatures on earth; they could readily escape by flight from their amphibian and reptilian enemies without danger of pursuit. Certainly the life of the insects must have been very different then from what it is now—with birds, bats, man, and DDT.

Our knowledge of the habits, life histories, and food of these early insects is necessarily slight, but certain inferences can be made from their structure, as we now know it. Let us see what this was like and what conclusions can be reached.

The order Palæodictyoptera, which existed during the Upper Carboniferous and Permian, is a negative and ill-defined group. Attempts to divide it into two or more orders have not proven successful, because some species seem to merge into the Ephemerida, and others into the Orthopteroids. Nevertheless, I believe that most of the one hundred fifty species which have been described are members of one order. Their closest living relatives are the Ephemerida and, to a lesser extent, the Odonata. The fact that all complete specimens are preserved with their wings outspread shows that, like the Ephemerida and Odonata, they were palaeopterous, i.e., unable to fold their wings back over the abdomen at rest. They had nearly similar fore and hind wings and were apparently weak fliers. Although they are mostly preserved as isolated wings, enough whole specimens have been found to give us a slight knowledge of their body structure. They were primitive insects, probably more so than any other known winged insects, but they did have some specializations. It should be noted, in this connection, that no remains of bodies of any insects have been found in the older half of the Upper Carboniferous strata. Not until we come to the Mazon Creek deposits, about 15 million years after the first record of the insects, are body remains known. This probably would have provided ample time for extensive specialization to develop. At any rate, the Palæodictyoptera were more primitive than any winged insects now living. They show about the same range in size as living dragonflies, many having a wing expanse of about two inches. The head was relatively small; the mouth-parts mandibulate and inconspicuous. Their antennæ are unknown, except for the proximal segments; probably they were moderately long and multisegmented. The thoracic segments and legs were nearly homonomous. The most striking characteristic of the Palæodictyoptera was the presence of paired membraneous lobes on the prothorax; these resembled miniature wings and are usually considered homologues of the functional meso- and metathoracic wings. The abdominal segments showed little differentiation, and the abdomen terminated in a pair of long, multisegmented cerci. Well preserved specimens have paired lateral lobes on each abdominal segment. The immature stages of the Palæodictyoptera are completely unknown. Several vague and fragmentary specimens, which are probably insect nymphs of some sort, have been assigned to the Palæodictyoptera, but they could just as well belong to certain other groups. The paired abdominal lobes of the adult have been generally interpreted as vestigial tracheal gills of the nymphs. This of course implies that the nymphs were aquatic; and in view of the close relationship between the Ephemerida and Odonata, both of which have aquatic nymphs, we may infer this to have been the case. From this you will see that our knowledge of the Palæodictyoptera is not great. Their general activities were probably much like those of the present-day may-flies, crawling and fluttering among the plants bordering the ponds or swamps in which their nymphs developed—inoffensive creatures whose only claim to fame is their antiquity and proximity to the great ancestor of all insects. They had no defense against the more powerful, predaceous insects which developed during the later Carboniferous and Permian, and for which they must have been easy prey.

Related to these Palæodictyoptera was another order of ephemerid-like creatures, termed the Megasecoptera. They were small to large insects, with a wing expanse ranging from one-half to five inches, and, like the Palæodictyoptera, they were unable to fold their wings over the abdomen. Until about 12 years ago they were known exclusively from the Upper Carboniferous; many Permian species have since been found, and it has become apparent that the order did not attain its greatest development until that period. They had moderately long antennæ, and extremely long cerci. In the Carboniferous species the head was small and short, but in some of the Permian types it was prolonged into a rostrum, probably much like that of the scorpion-flies. The older forms had mandibulate mouth-parts, and this was probably true also of the later species. The thorax and abdomen were slender, and, in the main, generalized in structure. In certain Carboniferous species, however, the prothorax was highly modified, bearing conspicuous projections or spines, which may have had some protective value. The legs of most were of the ordinary walking type, but in one Carboniferous genus (*Mischoptera*) the fore legs were short and raptorial in form though there are no other indications of predaceous habits. The wings were the most characteristic structures of the Megasecoptera. In most species they were very narrowed basally, and in one family they were arcuate, as in many families of living insects. Two abdominal structures are noteworthy: the very elongate cerci, which surpass in length those of most other insects; and, in certain families, lateral gill-like processes, resembling those of the Palæodictyoptera. Nothing is known of the immature stages of the Megasecoptera, but the presence of the supposed gill-vestiges just mentioned suggests that at least some of them had aquatic nymphs.

The Megasecoptera were probably no better fliers than the Palæodictyoptera, and their long cerci must have handicapped them in their attempts to escape from enemies. Perhaps this had something to do with their abrupt disappearance at the close of the Permian, for no sign of them has been found in later strata.

We next come to the insect dinosaurs—the Protodonata. These include the largest insects known, living or extinct. Although all species were large, as insects go, not all were giants, as is usually stated; some had a wing expanse of five inches, which is well within the limits of many living insects. Three very large species have been found, all belonging to the family Meganeuridæ. One, from the Carboniferous of France, was about twenty-six inches across the wings; the other two, from the Lower Permian of Kansas and Oklahoma, were somewhat larger, with a wing expanse of about thirty inches. The distribution of these species, both in space and time, indicates that the giant meganeurids inhabited an extensive area of the earth for some fifty million years, though the whole order became extinct shortly after the close of the Permian Period. The protodonates resembled dragon-flies in general appearance, and the earlier forms were probably directly ancestral to the true Odonata. They had large, toothed mandibles and spiny legs, and were undoubtedly predaceous. What they fed on, we can only guess. The contemporary slow moving Palæodictyoptera and Megasecoptera, which, because of their wing structure, were unable to hide easily among plants or under rocks, were probably their chief source of food. Protodonate nymphs are unknown. They were probably aquatic, although Dr. August Krogh has asserted that nymphs of the giant meganeurids could not have breathed through caudal or rectal tracheal gills, as odonate nymphs do, since in order to convey the necessary quantity of oxygen to the head, their tracheæ would have required a cross-section greater than that of the body itself. However, passage of oxygen in the tracheæ might well have been sufficiently aided by muscular movement to make this mechanism practical. At any rate, the adult Protodonata and Odonata are so much alike, I find it difficult to believe that their nymphs were very different.

The insects which we have been considering so far are primitive types which we would expect to find as part of early insect life. The group we are now to discuss is not in this category. For although their wings were of the palæopterous type, the head was modified into a long rostrum, with suctorial mouth-parts. The best preserved specimen (*Eugereon*) of this group has been found in Upper Permian rocks of Germany, but other representatives, also with elongate beaks, have been collected in Carboniferous strata of France, Belgium, and England. Since these insects were at first thought to have been related to the Hemiptera, Handlirsch termed the order the Protohemiptera. The choice of name was unfortunate, for, with the discovery of new specimens, it has become increasingly clear that they had nothing to do with the Hemiptera, but are instead closely related to the Palæodictyoptera. The order was obviously a widely distributed one, members having been found in Permo-Carboniferous strata of both Europe and North America; and specimens from Triassic rocks of Australia show that it persisted into the Mesozoic. The Triassic representatives, by the way, are remarkable in that the fore wings had a very large stridulatory area. The Palæozoic Protohemiptera had long cerci and well developed prothoracic wing lobes, like those of the Palæodictyoptera. The presence of suctorial mouth-parts raises the question of feeding habits. It is obvious from their modified mouth-parts that the Protohemiptera consumed liquid foods; whether this was plant juice, from such gymnosperms as lycopods, seed-ferns, and horse-tails, or the blood of reptiles and amphibians, is uncertain. But it is most interesting that as far back as the Upper Carboniferous, at least two hundred twenty-five million years ago, the suctorial mechanism had been developed in insects; and also that this device originated in relatives of the may-flies and dragonflies, quite independent of its subsequent development in the Hemiptera and the Diptera.

The largest extinct order of Carboniferous and Permian times was the so-called Protorthoptera. This included a bewildering variety of insects, suggestive of most of the orders to which we apply the term Orthopteroidea. Some show definite traces of characteristics found in the cockroaches, others recall the mantodean and even the saltatorial Orthoptera; but so far no satisfactory division of the Protorthoptera has been proposed. All of them were neopterous, i.e., folded their wings over the abdomen at rest. The more primitive types, however, possessed pronotal lobes, like those of the Palæodicty-

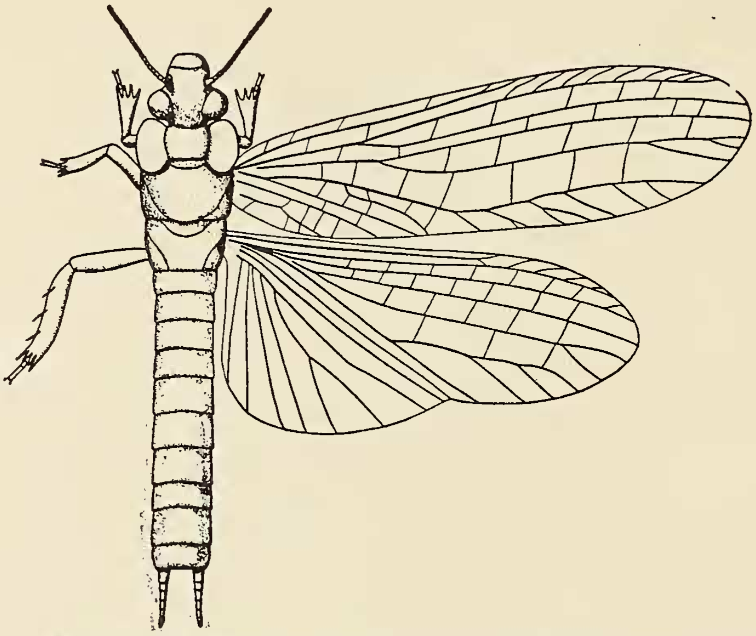

Figure 3. *Probnis speciosa* Sellards (Order Protorthoptera), from the Lower Permian of Kansas. Original restoration, based upon specimens in the Museum of Comparative Zoölogy.

optera. Their wings were unequal, the hind pair having an expanded and plicate anal area. In certain Permian species, and perhaps also some Carboniferous ones, the fore wings were tegminous and distinctly punctate. A prominent ovipositor and cerci were present in most species. Apart from the wings, the prothorax showed the greatest amount of diversity. In many Carboniferous species, the prothorax was long and even armed with large spinous projections, whereas in others this segment was small and inconspicuous. The legs also showed much diversity. The fore legs of some were clearly raptorial, long and armed with spines and teeth; in others they were curiously modified, perhaps for digging or climbing (Figure 3). The hind legs were specialized in some species for leaping, as in grasshoppers and crickets. It is apparent, therefore, that these early orthopteroids were a varied lot. They probably inhabited small seed-ferns, the phytophagous species feeding on the leaves and the predaceous ones on Palæodictyoptera and other defenseless insects. They were not very large creatures, though a few attained a wing-expanse of six inches. The nymphs

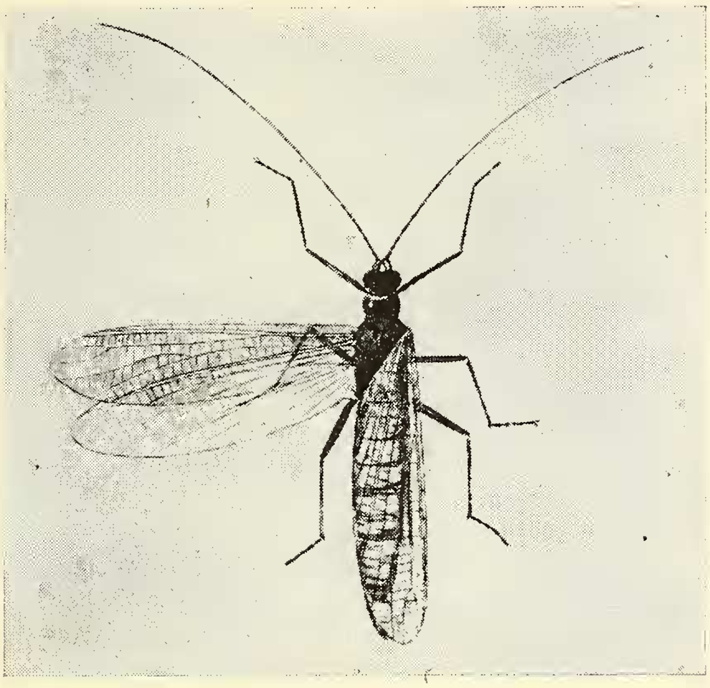

Figure 4. *Paleuthygramma tenuicornis* Martynov (Order Caloneurodea), from the Upper Permian of Russia. (After Martynov.)

of several families are known; they resembled the adults closely and were obviously terrestrial.

Related to the Protorthoptera, but different enough to require ordinal separation, were the Caloneurodea, which existed during the Upper Carboniferous and Permian periods. They were slender insects, with long antennæ and tenuate wings (Figure 4). The largest of them had a wing expanse of five inches. They differed from the Protorthoptera chiefly in having hind wings like the fore wings, with no enlargement of the anal area. In general appearance the caloneurodeans probably resembled the long-horned grasshoppers, except that their legs were cursorial, not modified for jumping. Their nymphs are unknown.

The extinct orders which we have been considering have had a geologic record extending throughout the Carboniferous and Permian. We now come to two orders which are known only from the Permian period. One of these, the Protoperlaria, is the best known of all the ex-

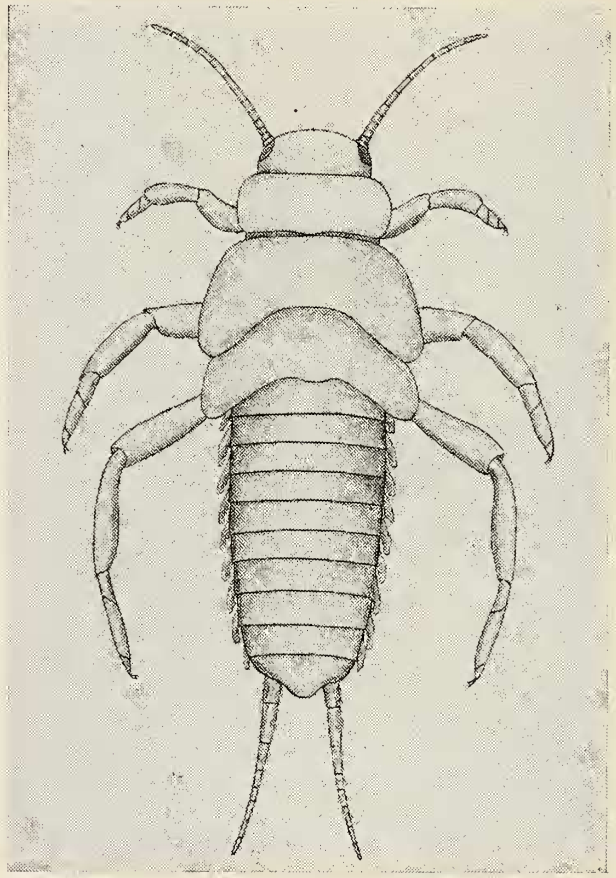

Figure 5. Protoperlarian nymph, from the Lower Permian of Kansas. Original restoration, based upon specimens in the Museum of Comparative Zoölogy.

tinct orders of insects, their remains being very abundant in Lower Permian rocks of Kansas and Oklahoma. The adults were similar to the existing stone-flies, but they had pronotal lobes like the Palæodictyoptera, five tarsal segments, and a distinct, though small, ovipositor. The abdomen had long cerci and nine pairs of vestigal lateral gills, recalling those of the Palæodictyoptera and some Megasecoptera. That they were vestigial gills is shown by the nymphs (Figure 5). These were well adapted to an aquatic life, with swimming legs, and the lateral abdominal gills.

The other extinct Permian order is the Protelytroptera, which includes the most highly modified of all the Paleozoic insects. They had true elytra, very thick and convex, though with vestiges of venation (Figure 6). The hind wings were large, with a greatly expanded anal region, and with hinges on the longitudinal veins enabling the wing to fold up transversely as well as lengthwise. In

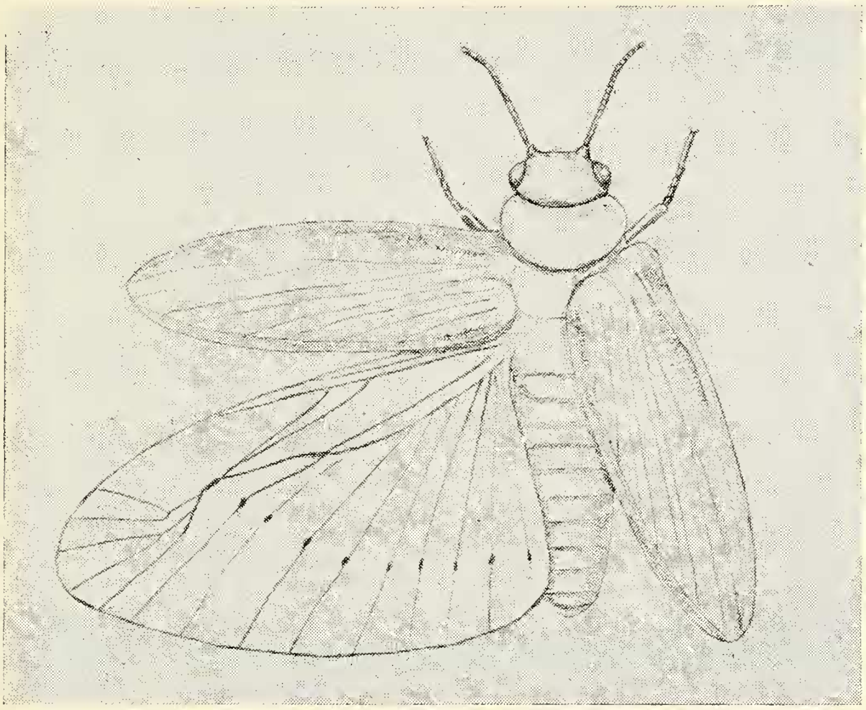

Figure 6. *Protelytron permianum* Tillyard (Order Protelytroptera), from the Lower Permian of Kansas. Original restoration, based upon specimens in the Museum of Comparative Zoölogy.

general appearance these insects were highly suggestive of beetles, but the venation of their hind wings shows clearly that they were not at all allied to the Coleoptera. They might be related to the roaches or to the Dermaptera, but most likely they represent an early and independent origin of the elytrophorous condition. Nothing is known yet of their mouthparts or of their immature stages.

The foregoing discussion has dealt only with the *extinct* insect orders of the Upper Carboniferous and Permian periods. Let us now turn to the living orders. As we noted earlier, although ten of these are known from Paleozoic rocks, only one has a record which goes back to the Upper Carboniferous—the Blattaria or cockroaches. Their oldest remains are found in early Westphalian strata, which were deposited about two hundred forty million years ago. These first specimens consist only of wings, but complete or nearly complete specimens have been found in late Westphalian and Stephanian rocks. It is clear from these fossils that even that early in the earth's history, the roaches were not very different from what they are now. They were flat, and had a broad pronotum and tegminous wings like modern types. The venation, also, was similar to that which occurs in many of our living species—so much so that it is not easy to find obvious differences between Carboniferous and existing members of the group. Nymphal forms and several egg cases, which have been found in Permian rocks, serve to emphasize their similarity. Roaches are the most abundant of all Carboniferous insects. However, this does not necessarily mean, as it has usually been interpreted, that they were the prevailing insects of the time; it merely means that they were numerous in a particular region or environment. Most insect-bearing rocks were first deposited as mud, and the roaches presumably thrived in moist or damp regions having a luxuriant plant growth. The picture we get from the fossils can therefore be misleading, for it gives us a conception of the local biota only; if we had equally good samples of the fauna of dry regions, we would probably find the roaches less numerous. The size of the Paleozoic roaches has also been erroneously described. Although the statement is often made that giant roaches lived in the Carboniferous, no fossil specimens have been found which exceed the size of some of our living species. It is true, of course, that the *average* size of fossil roaches exceeds that of the existing species; but that is because the large roaches had a better chance of being preserved as fossils than the small ones. This selective aspect of preservation is often overlooked.

Let us now consider the existing orders which first appear in the Permian. The best known of these is the Ephemerida or may-flies, remains of which have been found in the Lower Permian rocks of Kansas and Oklahoma, as well as in Upper Permian deposits of Russia. They were about the same size as living may-flies, with a wing expanse of less than two inches. Their antennæ were much longer than those of existing species, however, and the prothorax was slightly broadened, with an indication of membranous lobes in some species. The abdomen, which terminated in long cerci and a median caudal filament, closely resembled that of Recent members of the order. The wings were their most interesting structures. Living members of the order, and even those from Mesozoic rocks, have greatly reduced hind wings; but in the Permian species, the hind wings were about equal to the fore wings in size, and had nearly the same venation. Some of the specimens from the Lower Permian of Kansas are clearly in the subimaginal stage, showing that this distinctive phase of ephemerid metamorphosis occurred even in those early days. Several nymphs, found in the Permian of Oklahoma and Russia, have the characteristics of living ephemerids—swimming legs, caudal filaments, and lateral abdominal gills.

True Odonata are represented in Permian strata only by wings. They have been found in Permian rocks in North America, Russia and Australia. Most species were surprisingly small, a few being less than an inch and a half across the wings. Both dragon-fly and damsel-fly types were present in the Lower Permian. Their nymphs are unknown, but they were almost certainly aquatic.

The Corrodentia or bark lice are relatively common in Permian strata. Like existing species, they were very small and even minute, most having a wing expanse of about half an inch, some a quarter of an inch. The body structure of a few Lower Permian species is well known. The head was relatively large, with long antennæ and prominent eyes (Figure 7). Surprising enough, the anterior part of the head was prolonged into a short rostrum, but whether the mouth-parts were adapted for chewing or some other method of feeding has not been determined.

At any rate the maxillary and labial palpi were conspicuous and generalized in structure. Another interesting feature of the early psocids was their wings. In existing species the hind pair are much smaller than the fore, with a reduced venation, but in the Lower Permian species the fore and hind wings were alike. Some of the Upper Permian members show the beginnings of hind wing reduction. Presumably these small creatures had essentially the same habits as many modern species, living under

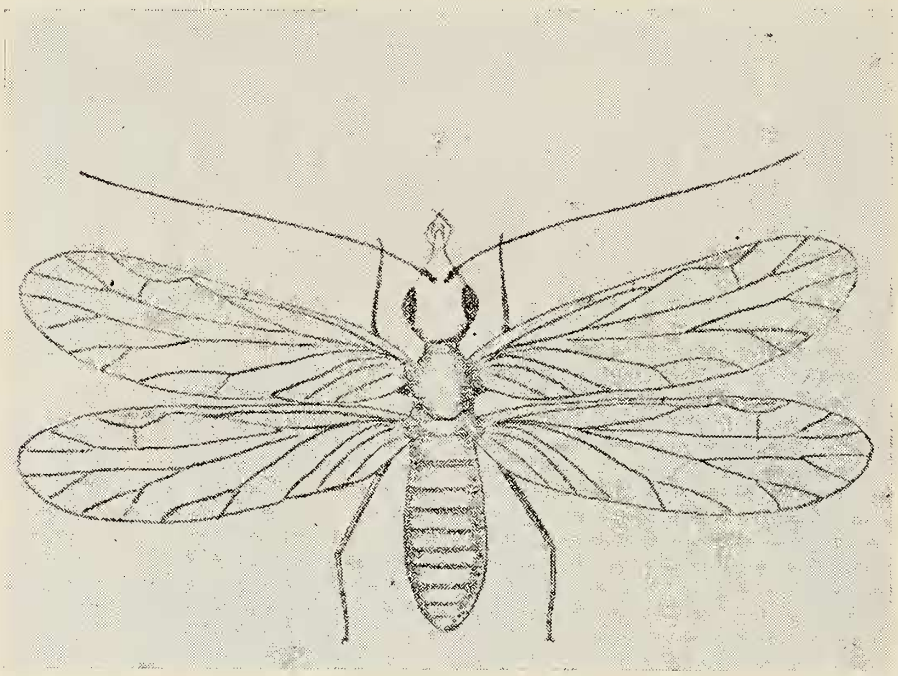

Figure 7. *Dichentomum tinctum* Tillyard (Order Corrodentia), from the Lower Permian of Kansas. Original restoration, based upon specimens in the Museum of Comparative Zoölogy.

bark of trees or in leaf mould—but the trees and leaves were very different from those now inhabited by their descendants.

All the true bugs, i.e., Hemiptera, of the Permian were members of the suborder Homoptera. Most of them were small, with a wing expanse of less than an inch, though in a few this reached two inches. The Lower Permian species were much less specialized than the Upper Permian ones, but they had the characteristic beak and maxillary and mandibular bristles of existing bugs. The wings are interesting because they were about equal in size, and because the hind wing had the venational features of psocid wings. The best known of the Lower Permian Hemiptera had a long, straight tube projecting from the end of the abdomen, but whether this was an ovipositor or respiratory tube remains to be determined. By Upper Permian time the Homoptera had developed a variety of families, some of them approaching certain existing families (Figure 8). There can be no doubt, on the basis of their known structure, that these early bugs had already settled down to a diet of plant juices.

We now come to the two remaining orders of insects which appear in the Lower Permian, the Mecoptera and Neuroptera. Their presence in Lower Permian rocks is

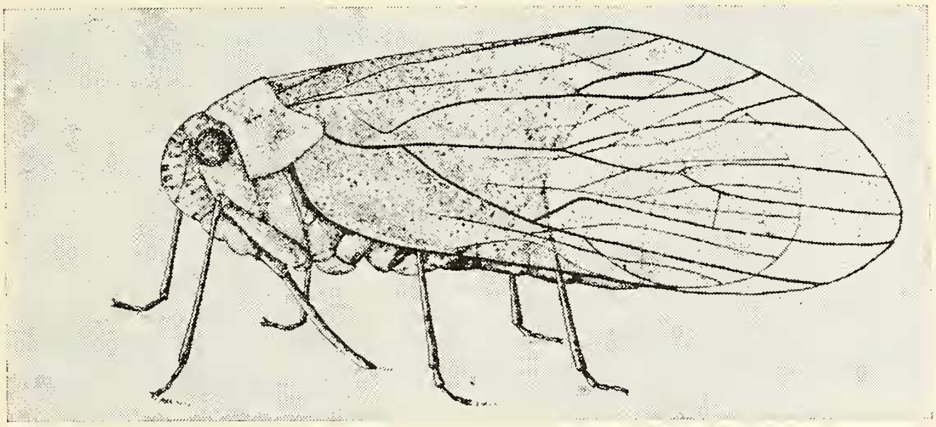

Figure 8. *Permocicada interga* Beck. (Order Hemiptera), from the Upper Permian of Russia. (After Becker-Migdisova.)

interesting and surprising. Since existing members of both these orders have complete metamorphosis, we can conclude that the Permian species also had that type of development—unless, of course, we grant that complete metamorphosis might have arisen independently in the two orders, which seems improbable. True larval forms have been found in Permian deposits of Kansas, but their ordinal affinities have not been determined with certainty. The Lower Permian Mecoptera, or scorpion-flies, were very small, with a wing expanse of about an inch, though some of the later Permian species were more nearly the size of existing members of the order. Their body structure was much like that of certain living genera, such as the Australian *Chorista,* the head including a short rostrum (Figure 9). During the late Permian, and, incidentally, the early Mesozoic, the Mecoptera were relatively abundant and diverse. In one Permian deposit in Russia the Mecoptera make up 20% of the insect fauna found there, though at the present time they comprise less than .05% of the world's insect fauna. The Neuroptera of the Permian are no less interesting than the scorpion-flies. Two distinct types occur in Lower Permian rocks—the Raphidiodea or snake-flies, and the Planipennia. Very little is known of their body structure, but their wings indicate that, whereas the Lower Permian snake-flies were primitive and closely related to existing families, the

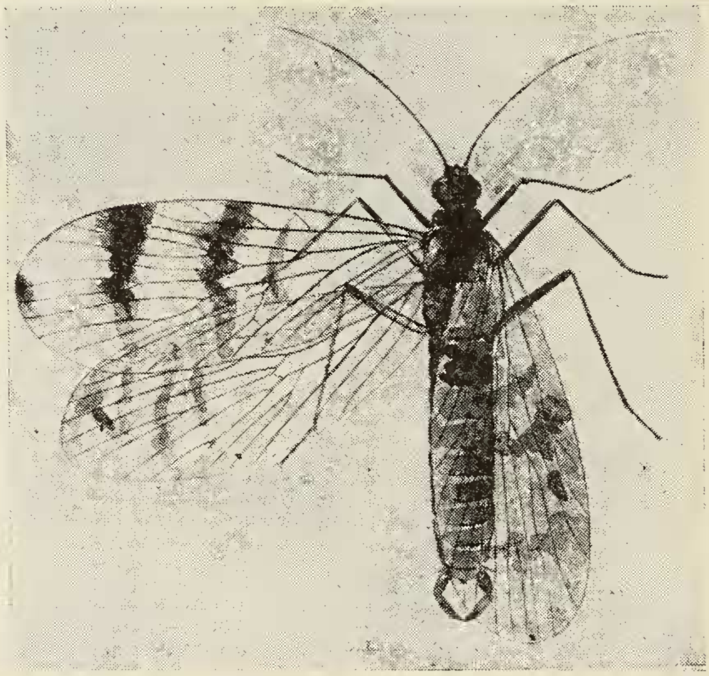

Figure 9. *Agetochorista tillyardi* Martynov (Order Mecoptera), from the Upper Permian of Russia. (After Martynov.)

Planipennia were highly specialized, and only remotely related to existing groups. In Upper Permian rocks, however, the Planipennia are represented by an extensive series of fossils which are close to certain living families, such as the Berothidæ, Sisyridæ, etc.

There remain to be considered now three other orders, two of which, the Thysanoptera and Perlaria, appear first in Middle Permian rocks, and the third, Coleoptera, in late Permian deposits. The earliest Perlaria have been found in Russian strata and although they are very fragmentary, their identification is substantiated by the presence of more definite specimens in late Permian rocks of Australia. The latter were considered by Tillyard as being very closely related to the existing Eustheniidæ of the Australian region. The Thysanoptera or thrips, also found in Russian deposits, are of course minute and the details of the wings are not known; but the fossils certainly show the general characteristics of the thrips.

The first unquestionable Coleoptera, or beetles, are found in the Upper Permian of Russia and Australia. Unfortunately, complete specimens are unknown, though several well preserved elytra have been found. The family relationships of the fossils cannot be ascertained on these structures alone; but several types of elytra are represented, including some which are alike those of the Cupedidæ, and others which recall those of the Hydrophilidæ. It should be noted that since beetles are very abundant in Triassic deposits, their presence in the Permian is not surprising.

This then, is a general picture of early insect life. Our knowledge of it is limited, and there are many gaps to be filled, but we do have some idea of its nature. In reality, two faunas existed during the geologic periods considered—a Carboniferous fauna and a Permian one. The contrast between these two is fully as great as that between the faunas of the Triassic and the present. Even by late Permian time, about one-third of all the living orders of insects had come into existence, and the abrupt appearance of so many existing orders in the Lower Permian suggests that some of them lived in Carboniferous time, though not yet found in strata of that period. This early insect fauna included both predators and plant feeders, some of which had suctorial mouth-parts. The metamorphosis of the Carboniferous species, so far as known, was of the incomplete type, some apparently having aquatic nymphs; but by early Permian time, complete metamorphosis had been acquired. All of this took place before the existence of flowers or mammals or birds—to say nothing of man. It is no wonder that the insects have such a tenacious hold on what we consider to be our planet.